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BIOLOGY OF *MICRODON FUSCIPENNIS* (DIPTERA: SYRPHIDAE) WITH INTERPRETATIONS OF THE REPRODUCTIVE STRATEGIES OF *MICRODON* SPECIES FOUND NORTH OF MEXICO

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Abstract.—Two hundred and ninety six adults, larvae, and pupae of *Microdon fuscipennis* were collected and/or reared from nests of the dolichoderine ant, *Iridomyrmex pruinosus* (Roger). Observations are made on the distribution of *M. fuscipennis* in the ant nests, sex ratio (1:1), adult emergence, mating, number of eggs laid ($\bar{x}$ = 63), larval emergence from the egg, and predation (third-instar fly larvae frequently eat ant larvae). Reproductive strategies for the genus *Microdon* are: 1) specialist strategy—one host species; and 2) generalist strategy—multiple host species. The species of *Microdon* found north of Mexico and their ant-associations are listed and used to predict the reproductive strategy of each fly species.

Microdons are unusual syrphid flies. The larvae and pupae are dome-shaped and develop in ant nests. The larvae exhibit slow, sluglike movements, a characteristic which originally caused them to be described as mollusks or coccids (Wheeler, 1908). As adults, microdons do not show typical syrphid behavior. They do not hover or visit flowers as most syrphids but spend their adult lives close to the ant colonies from which they emerged.

More than 350 species of *Microdon* are known from all zoogeographic regions. The diversity, greatest in the tropics (especially the Neotropics, 174 species), tapers off rapidly towards the poles. The northern- and southernmost records for microdons in the New World are *Microdon albiconatus* Novak from the Yukon (62°41′N) and *Microdon violaceus* (Macquart) from Chile (37°47′S). Microdons are considered primitive because they represent the first offshoot on the branch which includes all other syrphids (Thompson, 1969, 1972). The phylogenetic position and biologic distinctiveness of microdons clearly support the recognition of the group as a separate family (Thompson, 1969, 1972). For pragmatic reasons, however, microdons are left as an aberrant subfamily of the Syrphidae.

Early reviews on microdons (Wheeler, 1901, 1908; Donisthorpe, 1927)

were primarily descriptive, speculating on behavioral interactions between the larvae and their hosts. Andries (1912) first provided quantitative data on the life cycle of microdons as well as detailed descriptions of larvae, pupae, and adults. Greene (1955) added information on a number of *Microdon*-ant associations and described larval and pupal forms. More recently, Jordan (1968), and van Pelt and van Pelt (1972) contributed additional biological data (see Table 3). Akre et al. (1973) determined the sex ratio, size measurements, number of eggs laid per female, and the number of larvae and pupae per colony for two color morphs of *M. xanthopilis* Townsend (reported as *cothurnatus*), forming a sound basis for future comparative work on other *Microdon* species.

The biology of microdons is not uniform. Akre et al. (1973) described only one generation per year. *Microdon fuscipennis* (Macquart) has at least two. Akre et al. (1973) also stated that microdons overwinter as third larval instars, yet these data indicate that this is not true for *fuscipennis*.

Other unresolved questions exist. Are the microdon eggs laid in the ant nest or do the larvae move there? Do the microdon larvae eat the ant larvae and pupae?

These questions are discussed with respect to *M. fuscipennis* which develops in the nests of the dolichoderine ant, *Iridomyrmex pruinosus* (Roger). Two alternative behavioral strategies for *Microdon* flies are described. Table 2 lists the species of *Microdon* found in America north of Mexico and their known hosts and predicts their reproductive strategy.

Materials and Methods

Collection.—*Microdon fuscipennis* was collected primarily during the spring and summer near Athens, Georgia, from nests of *Iridomyrmex pruinosus*. Ant nests were excavated with a pen knife. *Microdon fuscipennis* larvae and pupae were placed in plastic pop-top vials for transport. Entire ant colonies were also transported back to the laboratory.

Laboratory rearing.—The fly larvae were reared in plastic ant nests, exposed to natural daylight, and stocked with ant colonies dug in the field. The ants were maintained on honey and mealworms. Water was supplied by means of cotton plugs inside the nests. After the microdon larvae were observed eating the young ant larvae, additional ant larvae were added weekly to the colonies.

As the microdon larvae grew and pupated, the pupae were removed and placed in vials. A wooden stick was placed in each vial allowing the teneral adults an elevated surface from which they could expand their wings. All live material was kept at 27°C.

As the adults emerged, the pupal cases were removed from the rearing vials and placed in capsules. When an adult died, it was pinned along with the pupal case.

Table 1. Quantitative data on *Microdon fuscipennis*.

	Mean	Standard Deviation	n
Number of *M. fuscipennis* larvae, pupae per *I. pruinosus* colony	3.45	3.75	84
Number of eggs laid per female	63.5	18.9	15
Sex ratio	1:1		

Groups of approximately 30 eggs were hatched in 3 cm × 3 cm vials, fitted with a secure top and a 0.5 cm charcoal-plaster (1:2) bottom for humidity control. Water was occasionally added. No fungal inhibitor was added. Although some containers supported rich fungal growth, egg mortality was low.

Results and Discussion

Field data.—Innumerable ant colonies of many different species were excavated. *Microdon fuscipennis* was found only in those of *I. pruinosus*.

Eighty-four *I. pruinosus* (Table 1) colonies containing microdon larvae and pupae were excavated. Over 20 additional nests contained only empty pupal cases. From the 84 colonies, 149 larvae, 141 pupae, and 6 adults were removed (296 total), giving an average of 3.5 microdons per colony. The largest number of microdons per colony was 24 (11 larvae, 12 pupae, and 1 adult). Between April and September, second and third larval instars and pupae could always be found in ant colonies. First-instars were also found from April to September, although very infrequently, perhaps because of their diminutive size and cryptic appearance. This suggests that *M. fuscipennis* reproduces all summer long. In contrast, *M. xanthopilis* has one generation per year (Akre et al., 1973). Premarked *Iridomyrmex* nests excavated in the winter revealed both second and third larval instars as well as pupae.

Laboratory data.—Reared adults had close to a 1:1 sex ratio, true also for *M. xanthopilis* (Akre et al., 1973).

Mating behavior.—Virgin females readily mated when placed with one male in the same vial. Although some females were unreceptive to a male, replacement with a second or third male eventually resulted in copulation. If mating resulted, it usually occurred within five minutes.

Soon after exposure to the female, the male would attempt to mount. Although no preliminary courtship was noted, *M. fuscipennis* adults emitted a "buzzing" sound when handled or first exposed to another individual. This phenomenon, common to many syrphid flies (Thompson, *in litt.*), was assumed to be defensive but may also be part of courtship. Frequently

several mounting attempts were made before copulation was successful. Mating position was similar to that described by Akre et al. (1973) for *M. xanthopilis*. The male prothoracic legs held the female's abdomen and the metathoracic legs were positioned on the tip of the female's abdomen. Frequently females were observed to stroke the male legs during copulation with her metathoracic legs. Copulation lasted from a few minutes to two hours. Both males and females readily mated more than once.

Oviposition.—Although a female mated soon after emerging from the pupal case, it usually took 24 hours before she oviposited. Females released eggs in batches of 4–5 in the rearing vials. If a small flat stone were placed in the mating vials, the female probed it with her ovipositor and then deposited the eggs beneath. Fifteen mated *M. fuscipennis* females deposited 925 eggs, averaging 63 eggs, with a maximum of 83 laid by one female (Table 1). Females reared from larvae laid as many eggs as those reared from pupae collected in the field. Eggs were usually laid within 48 hours and the female died within one day thereafter. *Microdon eggeri* Mik (Andries, 1912) and *M. xanthopilis* laid approximately 150 eggs per female (Akre et al., 1973). No field observations were made on oviposition of *M. fuscipennis*.

Eggs.—*Microdon fuscipennis* eggs were white, measured 0.7 mm × 1.5 mm, and had a distinctive sculpturing. Akre et al. (1973) found the eggs of *M. xanthopilis* to be much smaller (0.3 mm × 0.7 mm).

First larval instar.—First-instar larvae emerged through an elongated slit at the end of the egg between 7:00 and 9:00 AM. They were extremely mobile and demonstrated positive phototropism by moving toward the light in the rearing vial. Akre et al. (1973) observed similar behavior in *M. xanthopilis* and concluded that this mobility reflected a dispersal stage. This may be true, but it must also be noted that the problem of dessication is paramount for the first-instar since the surface to volume ratio is highest for them. Rapid movement into an ant nest would increase survival where the ground temperature (i.e. *M. fuscipennis*) is over 38°C. If the eggs are deposited and hatch outside the ant nest, rapid movement would be imperative for survival. When first-instars are found in the field, they are in the depths of the colony. These areas have few ants, are the moistest part of the colony during dry periods, and have fairly constant temperature during the summer. Thus, this factor may have an important role in the survival of the first-instars in their natural environment.

First-instars placed in ant nests had mortality rates of 90% or more. *Iridomyrmex* workers easily turned over the first-instar larvae and carried them out of the colony to the refuse piles where they desiccated and dried. If the colony had a surplus of food, the searching activities of the ants were diminished and the first-instars were not found as frequently. Second- and third-instars did not appear to be killed as frequently.

In artificial nests, the first-instar larva usually restricted its movements to

the moist cotton plug. The plug originally was clear of fungal growth but quickly became contaminated. First-instars did best in nests which had contained ants for a number of weeks prior to the introduction of the fly larvae, and which also had fungus-covered cotton plugs. First-instars were never observed eating ant larvae although they frequently moved among the young ant brood.

Second and third larval instars.—Second- and third-instars were primarily found near the young ant brood and appeared to be less dependent on moisture than first-instars. In field colonies, these larvae are found just below the surface where the ants move the brood to take advantage of the optimum ground temperature. Fly larvae developed more quickly in the field than in the laboratory because of the higher ambient temperatures and a more plentiful food supply.

In laboratory colonies, second- and third-instar larvae consumed half-grown ant larvae or smaller ones but never pupae. Frequently the ants would pull the larvae away from the microdon. Successful microdons moved up and over the ant larvae piercing the larval skin and emptying the body contents, then discarding the empty shell. A worker would promptly pick up the larval remains and carry it to the refuse pile. Frequently, third-instars were observed consuming 8–10 larvae in a 30 minute period. I have also observed *M. globosus* (Fabricius) feeding on ant larvae. Similarly van Pelt and van Pelt (1972) reported that *M. baliopterus* Loew consumed larvae of the myrmicine ant, *Monomorium*.

Third larval instars prior to pupation occasionally released a clear brown fluid. Whether this fluid originated from the oral or rectal openings was not determined. The ants seemed to be attracted to the fluid and would consume it immediately. What the ants did with this fluid afterwards was not determined. Fluid release was also observed in *M. globosus*.

First larval instars, source of food.—In contrast to second- and third-instars, first larval instars were never observed eating ant larvae. First-instars frequently moved among the young ant larvae and would probe them with their mouthparts but never appeared to puncture the larval skin.

The first-instar fly larvae may obtain some form of nourishment from the ant larvae. Some myrmecologists (G. and J. Wheeler, personal communication) believe that the brood of the colony represents the digestive organ of the colony. Ant larvae are fed masticated proteinaceous materials; these materials are broken down and digested by the ant larvae and by trophallaxis fed back to the adult workers. The probing by the first-instar larvae may cause the ant larvae to release a liquid food which the fly larvae consume. No data presently exist to support this hypothesis.

Pupae.—Pupae were primarily found close to the surface (2 cm or less) in the larger galleries of the nest. Frequently groups of 3–4 pupae (emerged and yet to emerge) were found together. In the process of excavating col-

Table 2. Behavioral strategies of North American *Microdon*.

	STRATEGY I Example: *M. fuscipennis*	STRATEGY II Example: *M. xanthophilis*
1. Characteristics of the ant host		
a. Host	one host species	multiple host species
b. Size of the host	small species	large species
c. Brood production	throughout the summer	one generation per summer
d. Number of queens per colony	multiple queens	one or multiple queens
2. Number of generations of flies	multiple generations	one generation
3. Rate of development of the fly larvae	fast	slow
4. Food source	ant larvae	unknown
5. Reproduction	fewer eggs (ex. 62); larger in size	many eggs (ex. 150); smaller in size
6. Distribution	restricted to a single host	widespread, not restricted to a single host

onies with no larvae, empty pupal cases were found from the previous year. These were packed with soil and if the soil was moist, showed various degrees of deterioration.

Adult emergence.—Adult emergence from the pupal case took less than 60 seconds and usually occurred between 7:00 and 9:00 AM. The teneral adults crawled to the highest object in the rearing vial and remained motionless for 1–2 hours. Expansion of the wings rarely took more than 5–10 minutes. During the first 1–2 hours after emergence the adult flies released a fecal droplet.

Reproductive strategies of Nearctic microdons.—A compilation[1] of known information on microdon flies indicates two different reproductive strategies. *Microdon fuscipennis* and *M. xanthopilis*, two species for which we have relatively complete biological data, illustrate these different strategies (Table 2).

Microdon fuscipennis exemplifies the first strategy. Adults lay fewer eggs and seem to specialize on one host ant. This host is small, widely distributed, with populous colonies, multiple queens and a large quantity of brood. These host colonies support on the average 3.5 microdons (i.e. *M. fuscipennis*). Due to a long period of brood production, the microdon is able to

[1] These tables should be cited as: Duffield, R. M. and F. C. Thompson, 1981, Behavioral strategies and ant associations of the *Microdon* species found north of Mexico. Tables 2 & 3 in Duffield . . . etc.

Table 3. *Microdon*-ant associations for North American species north of Mexico. Subfamilies of ants are Formicinae (F), Dolichoderinae (D), and Myrmicinae (M).

Species of *Microdon*	Host Ant and Subfamily	Reproductive Strategy	Reference
M. abditus Thompson		1	
M. abstrusus Thompson	*Formica exsectoides* Forel (F)	2	this study
M. adventitius Thompson		1	
M. albiconatus Novak	*Formica obscuripes* Forel (F)	2	Akre (*in litt.*)
	Formica fusca L. (F)		this study
M. aurulentus (Fabricius)		2	
M. baliopterus Loew	*Monomorium minimum* (Buckley) (M)	1	van Pelt and van Pelt, 1972
M. coarctatus Loew	*Aphaenogaster fulva* Roger (M)	1	Greene, 1955
	Monomorium minimum (Buckley) (M)		Greene, 1923a
M. cothurnatus Bigot	*Formica obscuripes* Forel (F)	2	Cockerell and Andrews, 1916
	Formica haemorrhoidalis Emery (F)		Knab, 1917
	Camponotus pennsylvanicus (DeGeer) (F)	2	this study
	?*Camponotus vicinus* Mayr (F)		Cole, 1923
	Camponotus novaeboracensis (Fitch) (F)		this study
	Formica subnuda Emery (F)		this study
M. craigheadii Walton		1	
M. diversipilosus Curran		1	
M. fulgens Wiedemann	*Polyergus lucidus* Mayr (F); slave—*Formica schaufussi* Mayr (F)	2	
	Camponotus abdominalis (Buckley) (F)		this study
M. fuscipennis (Macquart)	*Iridomyrmex pruinosus* (Roger) (D)	1	this study
M. globosus (Fabricius)	*Tapinoma sessile* (Say) (D)	1	Greene, 1955; this study
M. laetoides Curran		1	
M. laetus Loew		1	
M. lanceolatus Curran	*Formica argentea* Wheeler (F)	2	Cockerell and Andrews, 1916
M. manitobensis Curran		2	
M. marmoratus Bigot		1	

Table 3. Continued

Species of *Microdon*	Host Ant and Subfamily	Reproductive Strategy	Reference
M. megalogaster Snow	*Formica subsericea* Say (F)	2	Greene, 1923b; this study
M. newcomeri Mann		2	
M. ocellaris Curran	*Formica schaufussi* Mayr (F)	2	this study
M. painteri Hull	*Monomorium minimum* (Buckley) (M)	1	this study
M. piperi Knab	*Camponotus vicinus* Mayr (F)	2	Cole, 1923
	Camponotus sp. (F)		this study
	Camponotus herculeanus (L.) (F)		this study
M. ruficrus Williston	*Lasius* sp. (F)	2	this study
	Lasius alienus (Foerster) (F)		this study
M. rufipes (Macquart)	*Pheidole dentata* Mayr (M)	1	this study
M. scutifer Knab		1	
M. tristis Loew	*Camponotus pennsylvanicus* (DeGeer) (F)	2	Greene, 1955
	Camponotus novaeboracensis (Fitch) (F)		this study
M. viridis Townsend		1	
M. xanthopilis Townsend	*Formica obscuripes* Forel (F)	2	Akre et al., 1973

produce more than one generation a year. Fly larvae consume ant larvae and are able to grow and develop quickly. The distribution of species exhibiting this strategy depends on the distribution of the host ant. This strategy is common to those species in the south.

A second strategy is reflected by *M. xanthopilis*. The adults are larger, lay more eggs, and specialize on closely related ant species. The host is usually large with populous colonies which can support one hundred or more microdon larvae. Fly development is slow, with only one generation a year. The larval food source is unknown, but probably is not the ant larvae.

Notes on other *Microdon* species.—Table 3 lists the species of *Microdon* found in America north of Mexico. Host records are included. The species taxonomy is that of Thompson (1981), who jointly developed these tables[1]. Details on the new host associations will be found in Thompson (1981). The microdon species were assigned a reproductive strategy on the basis of the available information and our concepts of their phylogenetic relationships. For example, *Microdon albicomatus* Novak is assigned to strategy 2 as its host is a species of *Formica*. *Microdon abditus* Thompson is assigned to

strategy 1 as this species is closely related to *globosus* Fabricius, a strategy 1 species.

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Literature Cited

Akre, R. D., G. Alpert, and T. Alpert. 1973. Life cycle and behavior of *Microdon cothurnatus* in Washington (Diptera: Syrphidae). J. Kans. Entomol. Soc. 46: 327–338.

Andries, M. 1912. Zur Systematik, Biologie, und Entwicklung von *Microdon* Meigen. Z. Wiss. Zool. 103: 300–361.

Cockerell, T. D. A. and H. Andrews. 1916. Some Diptera (*Microdons*) from the nests of ants. Proc. U.S. Natl. Mus. 51: 53–56.

Cole, F. R. 1923. Notes on the early stages of the syrphid genus *Microdon* (Diptera). Pomona Coll. J. Entomol. Zool. 15: 19–20.

Donisthorpe, H. 1927. The guests of British ants. G. Routledge, London. 244 pp.

Greene, C. T. 1923a. A contribution to the biology of North American Diptera. Proc. Entomol. Soc. Wash. 25: 82–91.

———. 1923b. The larvae and pupa of *Microdon megalogaster* Snow. Proc. Entomol. Soc. Wash. 25: 140–141.

———. 1955. Larvae and pupae of the genera *Microdon* and *Mixogaster* (Diptera: Syrphidae). Trans. Am. Entomol. Soc. 81: 1–20.

Jordan, K. H. C. 1968. Biologische Beobachtungen an *Microdon* (Diptera: Syrphidae). Entomol. Ber. Pp. 15–18.

Knab, F. 1917. On some North American species of *Microdon* (Diptera: Syrphidae). Proc. Biol. Soc. Wash. 30: 133–144.

Pelt, A. F. van and S. A. van Pelt. 1972. *Microdon* (Diptera: Syrphidae) in nests of *Monomorium* (Hymenoptera: Formicidae) in Texas. Ann. Entomol. Soc. Am. 65: 977–978.

Thompson, F. C. 1969. A new genus of microdontine flies (Diptera: Syrphidae) with notes on the placement of the subfamily. Psyche (Camb. Mass.) 76: 74–85.

———. 1972. A contribution to a generic revision of the Neotropical Milesinae (Diptera: Syrphidae). Arq. Zool. (São Paulo) 23: 73–215.

———. 1981. Revisionary notes on Nearctic *Microdon* Meigen (Diptera: Syrphidae). Proc. Entomol. Soc. Wash. 83: 725–758.

Wheeler, W. M. 1901. *Microdon* larvae in *Pseudomyrma* nests. Psyche (Camb. Mass.) 9: 222–224.

———. 1908. Studies of Myrmecophiles III. *Microdon*. J. N.Y. Entomol. Soc. 16: 202–213.